Reproductive Parameters of the Kemp's Ridley Sea Turtle (*Lepidochelys kempii*) at Rancho Nuevo, Tamaulipas, Mexico

WAYNE N. WITZELL¹, ALFREDO SALGADO-QUINTERO², AND MANUEL GARDUÑO-DIONTE³

¹U.S. National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, Florida 33149 USA [E-mail: wayne.witzell@noaa.gov];

²Calle Cobalto 1105, Colonia Industrial, Morelia, Michoacan C.P. 58130 Mexico [E-mail: alfiesq@yahoo.com.mx];

³Instituto Nacional de la Pesca, Pitagoras 1320, Piso 3, Colima Santa Cruz Atoyac, Mexico, D.F. 03310 Mexico

[E-mail: mdionati@yahoo.com.mx]

ABSTRACT.—Reproductive parameters of critically endangered Kemp's ridley sea turtles (Lepidochelys kempii) were recorded at Rancho Nuevo, Tamaulipas, Mexico, during the 1999 and 2000 nesting seasons. Recorded parameters included: nesting turtle lengths and weights, clutch sizes and weights, and egg and hatchling lengths and weights. There was a trend for larger turtles to lay larger clutches. Nesting turtle weights and clutch sizes were smaller than originally recorded in the 1960s, and may be attributed to an increasing number of smaller neophyte turtles entering the population. The Kemp's ridley has a low mean reproductive rate but it is large relative to their mean body size. It is suggested that the low reproductive rate is offset by multiple clutches, short remigration period, early maturity, and high hatchling survival through mass nesting. There was a tendency for mass nesting to occur during windy days, when increased surf may trigger auditory, olfactory, and visual cues that initiate arribazon behavior.

KEY WORDS. - Reptilia; Testudines; Cheloniidae; Lepidochelys kempii; sea turtle; arribazon; reproduction; mass nesting; Mexico

The Kemp's ridley turtle (Lepidochelys kempii) was once the most abundant sea turtle in the Gulf of Mexico with an estimated 40,000 females nesting in one site in Tamaulipas, Mexico, in a single day in 1947 (Hildebrand, 1963). Unfortunately, this species had been reduced to critically endangered status by the 1970s due to intense exploitation of eggs and the incidental by-catch of turtles in commercial fishing trawls (Márquez, 1990, 1994; National Research Council. 1990). International efforts to conserve the Kemp's ridley have focused on the protection of nesting turtles and bycatch reduction in the Gulf of Mexico shrimp fleets, and little published information are available on recent reproductive parameters despite the intensive conservation efforts at the primary nesting beach. Some information was provided when the population was in severe decline (Chavez et al., 1967), and Rostal et al. (1997) provided more recent data from the late 1980s, but basic reproductive data have not been adequately updated in recent years. Reproductive information is necessary for estimating overall reproductive output and for developing demographic models.

Ridley turtles (*Lepidochelys* spp.) are different from other sea turtles because of their synchronized nesting, called *arribada* or *arribazon* (Spanish for "a great influx of fish to coasts or ports at certain seasons"), and Kemp's ridleys are unique because they nest diurnally and primarily on a single beach located in Tamaulipas, Mexico. An *arribazon* saturates the nesting beach with eggs (and hatchlings) and thereby may increase the chances of individual hatchling survival over solitary nesters due to prey satiation (McGinley, 1989; Eckrich and Owens, 1995). The physiological and environmental cues that trigger an *arribazon* are presently unknown. Hildebrand (1963) and

Márquez (1990, 1994) reported that *arribazons* frequently occurred on windy days, and suggested that wind speed may be an important cue in triggering mass nesting.

The purpose of this paper is to document recent Kemp's ridley turtle reproductive data, review recent nesting periodicity estimates, provide estimates of reproductive effort, and examine the effects of wind speed on the *arribazon*.

METHODS

The main nesting site of the Kemp's ridley turtle is a 30 km beach located at Rancho Nuevo, Tamaulipas, Mexico. The beach was patrolled using all-terrain vehicles three times daily, at 0700, 1100, and 1500 hrs during the 1999 and 2000 nesting seasons (March - September). Turtles encountered during these patrols were measured and flipper-tagged. The patrol also scanned turtles for Passive Integrated Tags (PIT) and/or applied PIT tags if scanners and tags were available. Nests were transplanted to the egg corral at the main camp. The patrol immediately returned to the camp if five or more turtles or nests were found and the camp immediately mobilized for an arribazon. During an arribazon, the beach was divided into approximately 4 km sections and each section was patrolled by two-person teams. Each team attempted to measure and tag all nesting turtles in their section. All located nests were then collected and transplanted to the egg corral when the arribazon was completed.

Reproductive data were opportunistically collected on 69 solitary nesting turtles during non-arribazon days. Minimum straight carapace lengths (medial notch to notch; SCL) were measured with vernier calipers and weights were taken to the nearest kg with a spring scale. A subsample of 20 eggs

(maximum diameter) and 20 hatchlings (SCL) were also measured and weighed from each clutch. Egg diameters and hatchling carapace lengths were measured with vernier calipers, and egg and hatchling weights were measured on an electronic scale (± 0.5 gm). Entire clutches were cleaned of sand with soft brushes and weighed on a mechanical triple beam balance scale. All measurements were performed by the same individual (ASQ) to reduce sampling bias. Average wind speeds (km/hr) were recorded daily at 1200 hrs on the beach at Rancho Nuevo from 6 March through 2 June 2000 with a hand-held wind meter (±3% of reading). Wind speeds were also recorded during mass nesting events. Mean egg volume was determined by using mean egg radius (derived from the mean egg diameter) in the formula for calculating the volume of a sphere, since Kemp's ridley eggs are round. Reproductive effort was estimated by two different meth-

RE₁ = clutch weight x clutch frequency RE₂ = egg volume x clutch size x clutch frequency / remigration interval

RESULTS AND DISCUSSION

Previous studies of Kemp's ridley reproductive biology are few and most are published in non-peer reviewed literature (e.g., Márquez 1994, 1990). Data are often difficult to interpret because there is often a general lack of background information such as sample sizes, measuring techniques, and years sampled. Furthermore, the data from Rancho Nuevo have usually been summarized and it is often difficult to tease out original data from specific years. These factors make it difficult to compare changes in reproductive values between years.

Reproductive Parameters. — All reproductive parameters measured during this study are presented in Table 1. Observed carapace lengths of 69 nesting turtles ranged from

Table 1. Reproductive parameters of Kemp's ridley sea turtles nesting at Rancho Nuevo, Mexico, 1999 and 2000.

	Mean	SD	Range	n
Turtle Length (cm) ^a	65.5	3.5	58.8-71.9	69
Turtle Weight (kg)	35.1	3.3	27-42	69
Clutch Size (# eggs)	100.7	19.2	57-143	69
Clutch Weight (kg)	2.6	0.8	1.4-4.4	69
Clutch Volume (liters)b	2.67		_	
Egg Diameter (mm)	37.0	8.2	31-42	1380°
Egg Weight (g)	29.0	3.3	20-37	1380°
Egg Volume (ml) ^d	26.5		_	
Hatchling Length (cm) ^a	40.7	7.0	35-46	420 ^b
Hatchling Weight (g)	15.1	1.7	13.5-17.5	420b
Incubation Period (days) ^c	50	_	46-57	3641
Emergence Success (%) ^e	67		43-79	6277
Internesting Interval (days)f	24.4	5.2	12-37	51

^aCarapace length is straight-line notch to notch (SCL)

58.8–71.9 cm (SCL) with a mean of 65.5 cm. Earlier measurements by Chavez et al. (1967) and Pritchard and Márquez (1973) did not state measurement methodologies so direct comparisons with these recent data are not possible. Mean weights of post-nesting turtles, however, appear to have decreased over the years, decreasing from 44.3 kg (n=17) in 1966 (Chavez, 1967) to 36.7 kg (n=45) in 1988 (Márquez, 1990), and to 35.1 kg (n=69) in 1999–2000 for the present study. This shows a 20.7% decline in average female body mass from 1966 to 2000. Márquez (1994) also reported a decrease in nesting turtle size from 1966 to 1994 but did not identify possible reasons for the decline.

The reproductive data collected during the present study are compared with those reported by Chavez (1967) collected in 1966 (Table 2). Unfortunately, Chavez et al. (1967) provided an incomplete data set and comparisons between the two studies are limited to clutch and egg sizes, and nesting turtle weights. Mean clutch size has apparently decreased from 110 eggs to 100 eggs and represents a considerable (9.1%) change. Interestingly, Rostal et al. (1997) reported mean clutch sizes of 106.8 (n = 21), 112.4 (n = 21)= 20), and 111.4 (n = 20) for 1988, 1989, and 1990, respectively. However, these annual variations may be due to small sample sizes and may not accurately reflect actual mean clutch size. Mean egg sizes reported by Chavez et al. (1967) were also larger in 1966 (39 mm) than reported here (37 mm) and is possibly a function of smaller turtles laying smaller clutches.

Changes in mean nesting weight, clutch, egg, and hatchling sizes suggest that the demographics of the Kemp's ridley nesting population at Rancho Nuevo have changed, undoubtedly due to the population crash that occurred in the 1950s through 1970s and the subsequent increase of the population that began in the early 1990s (Fig. 1). There is evidence that the Kemp's ridley is a relatively fast maturing species and females may reproduce as early as 8-11 years of age (Schmid and Witzell, 1997; Zug et al., 1997). Faster maturing turtles are able to reproduce at smaller sizes and, presumably, earlier ages. Temporal changes in mean turtle size and clutch size may indicate that a large number of neophyte turtles are entering sexual maturity as the population increases. This would explain the smaller nesting females, smaller clutches, and smaller eggs in the present study.

A positive correlation exists between female size and clutch size in many turtles (Moll, 1979; Congdon and Gibbons, 1985), including green, loggerhead, and hawksbill

Table 2. Comparison of mean reproductive values of Kemp's ridley sea turtles at Rancho Nuevo.

	Chavez et al. (1967)		Present Study	
Years Data Collected	1966	n	1999–2000	n
Turtle Weight (kg) Clutch Size Egg Diameter (mm)	44.3 110.0 39.0	17 271 221	35.1 100.7 37.0	69 69 1380

^bCalculated by 26.5 ml/egg x 100.7 eggs/nest / 1000

 ²⁰ eggs and hatchlings were measured and weighed per clutch
 Calculated from mean egg size using volumetric formula for a

^e Burchfield et al. (2001), hatchery incubated clutches.

 $f_n = 51$ turtles (seen nesting three times).

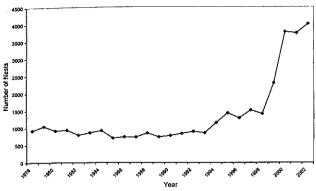


Figure 1. Nesting activity at Rancho Nuevo (Barra Ostionales to Barra del Tordo), 1978–2002. Nesting data are from Pritchard et al. (1978–1980) and Burchfield et al. (1981–2002).

sea turtles (Bustard, 1972; Hirth, 1980, 1997; Ehrhart, 1982; Witzell, 1985; Frazer, 1985; Frazer and Richardson, 1985, 1986; Dodd, 1988; Bjorndal and Carr, 1989; Hays and Speakman, 1991; Iverson, 1992; Van Buskirk and Crowder, 1994; Tiwari and Bjorndal, 2000). This relationship is often most significant between nesting populations, but it is often less obvious within nesting populations. Rostal et al. (1997) reported a weak relationship between carapace length and clutch size for Kemp's ridleys but did not provide any other correlation analyses. Regression analyses were performed on the data from our observed 69 turtles to determine turtle size and reproductive effort relationships. Positive relationships were found for four regressions (Fig. 2), and ANOVA indicated that turtle weight and clutch weight provided the most significant relationship (p = 0.002). Although egg sizes are usually relatively constant, variations in clutch sizes and frequency usually remain unexplained (Hays and Speakman, 1991). Perhaps these are due to differences in individual fitness in which a turtle can acquire enough resources to produce sufficient clutch mass.

Size at maturity is an important parameter in demographic models. Size data on adult male Kemp's ridley turtles are extremely rare. Nine male turtles were captured for a satellite tracking experiment (Burchfield et al., 2000). The curved carapace measurements were converted to straight line (nuchal notch to tip of posterior marginal scute) after Schmid and Witzell (1997). The resulting mean SCL was $60.5\,\mathrm{cm}\,(\pm\,5.8)$ and these carapace lengths were comparable to male turtles stranded at Rancho Nuevo (Burchfield et al., 2001), suggesting that male turtles may be smaller than nesting females. However, the sample size was small with a large standard deviation and $60.5\,\mathrm{cm}\,\mathrm{SCL}$ may not accurately reflect mean male size.

Renesting Intervals. — The number of nests per turtle per season and the number of years between successive nesting seasons are important parameters for population modeling and for determining total reproductive effort. Tagging data are commonly used to estimate these parameters for sea turtles, but tagging has numerous problems that can bias results. Incomplete beach coverage, tag loss, inoperative PIT tag readers, and small sample sizes can provide inaccurate results (Chaloupka and Musick, 1997). Estimates of the number of nests per turtle per season (n/t/s) for Kemp's ridley turtles have ranged from 1.32 to 3.00 (Table 3). The estimate of 3.00 n/t/s by Rostal (1991) using ultrasound data from nesting turtles on the beach is perhaps the best estimate because this technique uses non-biased physiological information and eliminates the problems inherent with tagging studies.

The remigration interval (number of years between nesting seasons) is another important parameter that is also difficult to determine due to the problems of using tag/recapture data previously mentioned. The remigration interval is important in estimating female population sizes but it is often variable in other cheloniid species (Hays, 2000;

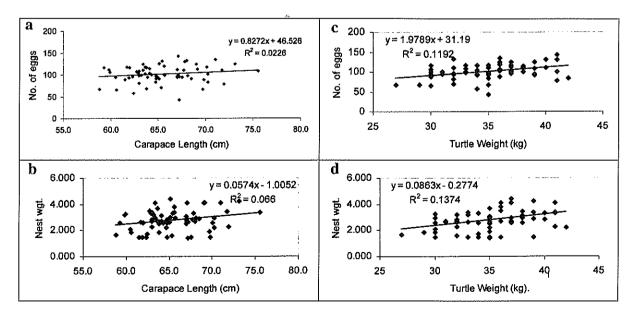


Figure 2. Regression analysis of turtle weight vs. clutch weight. ANOVA results for each regression: a) F = 1.502, p = 0.224; b) F = 4.590, p = 0.035; c) F = 8.795, p = 0.004; c) F = 10.356, p = 0.002.

Table 3. Reported nesting frequencies for Kemp's ridley sea turtles.

Nests per turtle per season	Source		
1.32	Márquez et al. (1982)		
2.00	Márquez et al. (1996)		
2.31	Pritchard (1990)		
2.70	USFWS & NMFS (1992) ^a		
3.00	Hildebrand (1963)		
3.00	Rostal et al. (1997)		
Remigration interval (years)			
1.75	Pritchard and Marquez (1973		
1.80	Present study		

^aDeveloped by averaging Rostal et al. (1997) and Pritchard (1990)

Solow, 2001). Tagging data were examined from 1996-2001 to estimate the remigration interval. These data were used because there were sufficient numbers of nesting turtles and because it was felt that these data were the most complete, with excellent flipper tag and PIT tag coverage of most nesting turtles. One hundred tagged nesting turtles randomly selected from the 1996 nesting season were observed to have renested for a total of 134 remigration intervals between 1996 and 2001. There were 38 one-year intervals, 83 twoyear intervals and 13 three-year intervals recorded, resulting in an average of 1.80 years between nesting seasons (Table 3). This is a relatively short remigration interval compared to other cheloniid species and is possibly due to a highly carnivorous diet and higher trophic level as suggested by Broderick et al. (2001).

Reproductive Effort. — The following method describes the reproductuve effort in terms of mean total egg mass produced per turtle per season. The parameters used are: mean clutch weight of 2.6 kg (present study) and 3.0 nests per turtle per season (Rostal, 1991; Rostal et al., 1997):

 $RE_1 = 2.6 \text{ kg x } 3.0 \text{ nests/turtle/season} = 7.8 \text{ kg/turtle/season}$

This reproductive effort is relatively small compared to other cheloniid sea turtle species (Table 4). This is not surprising considering the small mean size of the Kemp's ridley at maturity. However, when expressed as a percentage of the mean nesting weight the Kemp's ridley deposits the largest percentage of its body mass each nesting season. The duration of the remigration interval between nesting seasons is undoubtedly determined by how fast the turtles can replenish energy reserves necessary for egg production (Hays, 2000; Solow, 2001; Broderick et al., 2001). The Kemp's ridley is a carnivorous, fast maturing, and relatively short-distance migrating species that may be able to replenish protein and energy reserves faster, and/or more efficiently, than the herbivorous, slower maturing, long-distance migrating green turtle (Chelonia mydas). This may account for the relatively short remigration interval of 1.8 vrs for the Kemp's ridley.

The following method expresses total reproductive effort as the total volume (liters) of eggs produced per turtle per year, as described by Van Buskirk and Crowder (1994). The parameters used are: 26.5 ml/egg (estimated from present study), 100.7 eggs/nest (present study), 3.0 nests/ season/turtle (Rostal, 1991; Rostal et al., 1997), and 1.8 years remigration interval (present study):

 $RE_2 = 26.5 \times 100.7 \times 3.0 / 1.8 = 4.44$ liter eggs/year/female

Van Buskirk and Crowder (1994) estimated a slightly lower volume (4.07) for Kemp's ridleys. The differences in reproductive output values result from differences in the reproductive parameters used between our study and those used by Van Buskirk and Crowder (1994). Our study used smaller values for egg volume (26.5 vs. 30.8 ml) and clutch size (100.7 vs 110), and larger values for clutch frequency (3.0 vs. 1.8) and remigration interval (1.8 vs. 1.5).

Mass Nesting. - Wind speed and nesting data obtained from the 2000 nesting season at Rancho Nuevo are presented in Fig. 3. Linear and logarithmic correlation analyses of the nesting data indicate a positive, but weak, correlation with wind speed (Fig. 4). The weak correlations may be due to the cyclical nature of egg production or may be obscured due to the species' extremely decimated status. We then compared wind speed on days with and without arribazons, arbitrarily defined here as 100 or more nests at Rancho Nuevo on a single day. Mean wind speed during the entire study was 14.4 kph (\pm 8.9), but was 12.7 kph (\pm 7.5) for days with less than 100 nests (n = 81) and 26.0 kph (± 9.2) for arribazon days (n = 8), and indicates that arribazons tend to occur on windier days.

A highly variable internesting interval would enable the Kemp's ridley to delay egg deposition until the appropriate environmental cues trigger mass nesting. This internesting

Table 4. Seasonal reproductive effort of Kemp's ridley, green, loggerhead, and hawksbill sea turtles.

Species	Mean Clutch Weight (kg)	Mean Clutch Frequency	Mean Reproductive Effort (kg/yr)	Mean Turtle Weight (kg)	Mean Reproductive Effort (%) ^a	
Lepidochelys kempii	2.6	3.0	7.8	35.1	22.2	
Eretmochelys imbricata ^b	2.9	3.0	8.7	49.5	17.6	
Caretta caretta ^b	4.6	3.5	16.1	100.7	15.9	
Chelonia mydas ^b	4.4	5.5	24.2	126.7	19.1	

^a Reproductive effort (kg/yr) expressed as a percentage of mean weight

^b Reproductive data are from Australian C. mydas and C. caretta turtle populations (Hirth, 1997; Dodd, 1988) and from New Guinea E. imbricata turtles (Witzell, 1983)

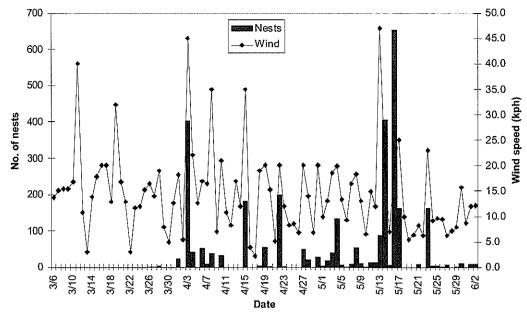


Figure 3. Daily wind speed and numbers of Kemp's ridley nests at Rancho Nuevo, Mexico, 2000.

interval was initially estimated to be 20–28 days (Pritchard and Márquez, 1973). The range (9 days) indicates some flexibility between successive nests since ovulation and egg production occur well before nesting (Owens, 1997). Fiftyone turtles that were seen nesting 3 times during the 2001 season (with both flipper and PIT tags) were randomly selected to determine their internesting interval. The resultant mean internesting interval of nesting Kemp's ridley turtles during the 2001 season was 24.4 days with a range of 12–37 (range, 26 days), and is similar to the 25-day internesting interval reported by Rostal et al. (1997). This

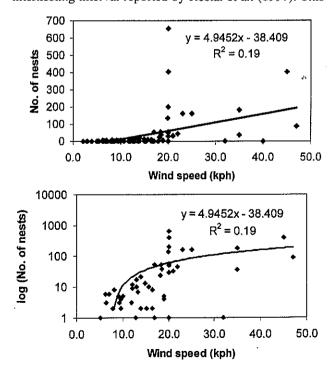


Figure 4. Linear (A) and logarithmic (B) correlation regressions of daily wind speed vs. numbers of nests at Rancho Nuevo, Mexico, 2000.

range (26 days) suggests that the turtles may be able to wait to nest several days for a suitably windy day. However, the turtles are still regulated to some degree by the cyclic nature of egg production and may not always be able to nest on windy days (Fig. 3). The internesting interval for Kemp's ridleys is longer than other cheloniid species: Chelonia mydas = 13-14 days (Hirth, 1997), Caretta caretta = 14 days (Dodd, 1988), and Eretmochelys imbricata = 15-18 days (Witzell, 1983). The exception is the olive ridley (Lepidochelys olivacea), another arribazon nesting species (nocturnal), which has an internesting interval of about 28 days (Kalb and Owens, 1994). These authors also suggested that the longer internesting interval for olive ridleys was possibly influenced by unknown external environmental cues. Owens and Morris (1985) reported that both ridley species produced eggs as rapidly as the other sea turtles, but developed the ability to hold clutches until conditions for an arribazon were right.

We suggest that increased wind speed may provide auditory, olfactory, and visual cues to stimulate mass turtle nesting. Kemp's ridley turtles are capable of hearing low frequency sounds and it has been hypothesized that sound served as a cue to initiate nesting (Lenhardt et al., 1983). The low frequency sounds generated by large surf on the nearshore sandbars would carry for many kilometers and bring turtles closer to the beach from distant offshore internesting habitats (Mendonca, 1986). Kemp's ridleys also have an acute sense of smell (Grassman, 1993), and the turbid water produced by large surf on the sandbars could provide olfactory cues from the beach. The visual effects of the surf would act as the final trigger to bring the animals over the sandbars to the beach. Kemp's ridleys also nest very quickly, the entire process sometimes as fast as 35-45 minutes (WNW, personal observations). This speed would help prevent heat stress during diurnal nesting. There are several evolutionary advantages of mass nesting on windy days at Rancho Nuevo.

The strong wind would help cool the turtles in the hot tropical sun and keep them from overheating, and would also hide the turtle tracks and spread nesting odors to confuse nest predators. Therefore, selection pressure would favor fast females that nest communally on windy days.

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